Quantitative macroscopic anatomy of the giraffe (giraffa camelopardalis) digestive tract

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Abstract: Quantitative data on digestive anatomy of the world's largest ruminant, the giraffe, are scarce. Data were collected from a total of 25 wild-caught and 13 zoo-housed giraffes. Anatomical measures were quantified by dimension, area or weight and analysed by allometric regression. The majority of measures scaled positively and isometrically to body mass. Giraffes had lower tissue weight of all stomach compartments and longer large intestinal length than cattle. When compared to other ruminants, the giraffe digestive tract showed many of the convergent morphological adaptations attributed to browsing ruminants, for example lower reticular crests, thinner ruminal pillars and smaller surface area of the omasal laminae. Salivary gland weight of the giraffe, however, resembled that of grazing ruminants. This matches a previous finding of similarly small salivary glands in the other extant giraffid, the okapi (Okapia johnstoni), suggesting that not all convergent characteristics need be expressed in all species and that morphological variation between species is a combination of phylogenetic and adaptational signals.

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Title: Quantitative macroscopic anatomy of the giraffe (*Giraffa camelopardalis*) digestive tract

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Summary

Quantitative data on digestive anatomy of the world's largest ruminant, the giraffe, are scarce. Data were collected from a total of 25 wild caught and 13 zoo housed giraffes. Anatomical measures were quantified by dimension, area or weight, and analyzed by allometric regression. The majority of measures scaled positively and isometrically to body mass. Giraffes had lower tissue weight of all stomach compartments and longer large intestinal length than cattle. When compared to other ruminants, the giraffe digestive tract showed many of the convergent morphological adaptations attributed to browsing ruminants, e.g., lower reticular crests, thinner ruminal pillars and smaller surface area of the omasal laminae. Salivary gland weight of the giraffe, however, resembled that of grazing ruminants. This matches a previous finding of similarly small salivary glands in the other extant giraffid, the okapi (*Okapia johnstoni*) suggesting that not all convergent characteristics need be expressed in all species and that morphological variation between species is a combination of phylogenetic and adaptational signals.

Introduction

Our current knowledge of the digestive anatomy and physiology of ruminants is generally based on a few but thoroughly studied livestock species, while only selective descriptions and scant quantitative data are available for non-domestic species. Domestic ruminants are grazers or intermediate feeders according to the classification introduced by Hofmann and Stewart (1972) and have 'cattle-type' digestive tracts according to a more recently proposed classification of ruminants as either 'cattle-type' or 'moose-type' based on digestive tract anatomy and physiology (Clauss *et al.*, 2010a; Dittmann *et al.*, 2015). Briefly, 'cattle-type' ruminants have stratified rumen contents, a fast reticuloruminal fluid throughput, a relatively large omasum, deep reticular crests and thick rumen pillars. In contrast, 'moose-type' ruminants have homogenous rumen contents, a slower fluid throughput, a relatively small omasum, low reticular crests and thin rumen pillars (Clauss *et al.* 2010a). Whereas 'moose-types' are usually strict browsers, 'cattle-types' may include varying amounts of grass in their diet to the effect that they are either considered strict grazers or mixed feeders (Codron and Clauss, 2010). The difference between these two types is currently thought to be related to a difference in the amount and viscosity of saliva they produce: whereas the 'moose-type' is thought to produce lesser amounts of a more proteinaceous (and hence viscous) saliva due to the inclusion of tannin-binding proteins, the 'cattle-type' produces larger amounts of a more watery saliva (Hofmann *et al*. 2008). The success of the 'cattle-type' is thought to lie in the more intensive harvest of microbes growing in the rumen by the increased 'wash-out' effect of the high fluid throughput (Dittmann *et al*. 2015). Of the browsing or 'moose-type' ruminants, only the moose (*Alces alces*) and roe deer (*Capreolus capreolus*) have been studied in detail (e.g., Hofmann *et al.*, 1976; Hofmann and Nygren, 1992a, 1992b), while comprehensive information on the world's largest ruminant, the giraffe, is scarce. A few reports provide quantitative data on the digestive anatomy of the giraffe (e.g., Hofmann, 1973; Maloiy *et al.*, 1982; Pérez *et al.*, 2009), but these studies are generally based on very few individuals or lack information about body mass (BM). A more comprehensive quantitative description of the digestive system of the giraffe would allow a better comparison of giraffes to other ruminants such as cattle, and facilitate a more detailed understanding of the overall comprehension of the evolutionary diversification of ruminants.

The first aim of this study was to provide solid data on the gross anatomy of the gastrointestinal tract of the giraffe using selected measures previously used to describe the ruminant digestive system (e.g., Hofmann, 1973; Clauss *et al.*, 2005, 2006a) and to determine the scaling relationship between BM and these anatomical measures. It was hypothesized that measures would scale isometrically to BM, i.e., linear dimensions to $BM^{0.33}$, area measurements to $BM^{0.67}$, and weight measurements to $BM^{1.00}$ based on simple geometric considerations (Peters, 1983). Further, it was hypothesized that the digestive system of the giraffe would show morphological adaptations similar to those described for ruminants with a 'moose-type' digestive tract, and be notably different from ruminants with a 'cattle-type' digestive tract . Therefore, the second aim of this study was to test this hypothesis through comparison with other ruminant species.

Materials and methods

Data were collected from 25 wild and 13 captive giraffes, though not every measure was obtained from every individual due to practical limitations or time constraints. Due to logistical considerations, the wild giraffes were caught in South Africa or Namibia and housed by Wildlife Assignments International Ltd, Hammanskraal, South Africa, for approximately 2 months before the dissection. During this period, the giraffes were group housed and received a diet of fresh locally cut savanna browse, leafy lucerne hay, and Boskos™ pellets (WES Enterprises (Pty) Ltd., South Africa). Water was freely available. The wild giraffes were all euthanized following physiological experiments conducted by the Danish Cardiovascular Giraffe Research project. Permission for euthanasia was granted by the Gauteng Province of South Africa.

Zoo giraffes from six Danish and one Swedish zoo were either culled for management reasons or because of chronic lameness due to osteoarthritis. These animals were fed diets consisting of hay (mainly alfalfa, but in a few cases grass-based), various concentrate pellets and as much browse as possible. Limited amounts of other feeds including Boskos^{TM} pellets, beet pellets, linseeds, oats, maize and various fruits and vegetables were used by individual institutions. Two newly born zoo giraffe calves were opportunistically included in the study. One was euthanized because of severe trauma, the other died perinatally.

Giraffe taxonomy is in flux, but using current nomenclature (Brown *et al.*, 2007), 3 subspecies of giraffes, as well as 5 hybrids were represented in the study. Demographic information about individual giraffes is listed in Table 1.

The dissection protocol was initiated within 30 minutes of euthanasia of the animals, except for the two giraffe calves, which were stored overnight at 5°C degrees prior to dissection. BM was obtained by weighing the giraffe in an upright position, using straps and a hanging electronic scale. After weighing, the digestive organs were removed from the body and the different sections were separated by ligating at the points depicted on Figure 1. Prior to measuring and weighing of the various gastrointestinal (GI) sections, the mesentery, adipose tissue and lymph nodes were removed. Considerable efforts were put into a meticulous dissection ensuring an almost complete trimming of all organs prior to data collection. Measures of rumen height, rumen diagonal, dorsal and ventral rumen length, reticulum height and length, omasum height, length and curvature, as well as the greater and lesser abomasal curvature (Figure 2) were taken before separating the omasum and abomasum from the reticulorumen. Subsequently, each stomach section was emptied, rinsed with water, and allowed to dry-drip for at least 15 minutes before empty weight was recorded. Internally, maximum reticular crest height and ruminal pillar thickness were recorded. Length of the intestinal sections (small intestines; SI, cecum, and large intestines; LI) were determined while containing digesta. The intestines were laid out in loops on a wet surface with minimal stretching, to measure the length. Each section was then emptied by squeezing out the content and weighed without rinsing. The empty and cleaned omasa were stored frozen before dissection of the omasal leaves. Upon dissection, the omasal leaves were scanned using a flatbed office scanner (HP Inkjet 2100, Hewlett-Packard, Palo Alto, CA, United States) and the omasal laminar surface area was determined using specifically developed image analysis software in MATLAB, version 7.10 (The Mathworks, Inc., Natick, Massachusetts, United States, 2010). Before weighing the parotid and mandibular salivary glands, surrounding fasciae, as well as the parotid lymph nodes, were carefully removed.

Data on digestive tract anatomy of other species of ruminants were compiled from the literature and classified as having either a 'moose-type' or 'cattle-type' digestive tract (Clauss *et al.*, 2010a) based on feeding ecology, and digestive tract anatomy and function.

'Cattle-type' ruminants (sorted alphabetically within subfamilies) included in the comparative analysis were: *Bison bison* (American bison), *Bison bonasus* (European bison), *Bos gaurus* (gaur), *Bos javanicus* (banteng), *Bos primigenus indicus* (zebu), *Bos taurus* (domestic cattle), *Boselaphus tragocamelus* (nilgai), *Bubalus bubalis* (water buffalo), *Bubalus depressicornis* (anoa), *Syncerus caffer* (African buffalo), *Alcelaphus buselaphus* (hartebeest), *Alcelaphus buselaphus caama* (red hartebeest), *Alcelaphus lichtensteini* (Liechtenstein hartebeest), *Beatragus hunteri* (hirola), *Connochaetes gnou* (black wildebeest), *Connochaetes taurinus* (blue wildebeest), *Damaliscus lunatus* (tsessebe), *Damaliscus pygarus* (bontebok), *Damaliscus pygarus phillipsi* (blesbok), *Addax nasomaculatus* (addax), *Hippotragus equinus* (roan antelope), *Hippotragus niger* (sable antelope), *Oryx beisa* (beisa oryx), *Oryx dammah* (scimitar oryx), *Oryx gazella* (gemsbok), *Oryx leucoryx* (Arabian oryx), *Capra hircus* (domestic goat), *Ovibus moschatus* (muskox), *Ovis ammon musimon* (mouflon), *Ovis aries* (sheep), *Ovis orientalis laristanica* (Laristan mouflon), *Kobus ellipsiprymnus* (waterbuck), *Kobus kob* (Uganda kob), (*Kobus leche kafue*) (Kafue lechwe), *Kobus vardoni* (puku), *Redunca arundium* (Southern reedbuck), *Redunca fulvolufula* (Mountain reedbuck), *Redunca redunca* (Bohor reedbuck), *Antilope cervicapra* (blackbuck), *Ourebia ourebi* (oribi), and *Elaphurus davidianus* (Pére David's deer).

'Moose-type' ruminants (sorted alphabetically within subfamilies) included in the comparative analysis were: *Tragelaphus angasi* (nyala), *Tragelaphus euryceros* (bongo), *Tragelaphus imberbis* (lesser kudu), *Tragelaphus scriptus* (bushbuck), *Tragelaphus strepsiceros* (greater kudu), *Pelea capreolus* (grey rhebok), *Litocranius walleri* (gerenuk), *Neotragus moschatus* (suni), *Oreotragus oreotragus* (klipspringer), *Muntiacus muntjak* (Indian muntjac), *Muntiacus reveesi* (Reeve's muntjac), *Muntiacus reveesi micrurus* (Formosan Reeve's muntjac), *Capreolus capreolus* (roe deer), *Mazama americana* (red brocket), *Mazama gouazoubira* (brown brocket), *Odocoileus hemionus* (mule deer), *Odocoileus virginianus* (white-tailed deer), *Alces alces* (moose), giraffe, and *Okapia johnstoni* (okapi).

The comparative literature data were collated from Tamate *et al.* (1962), Tulloh (1966), Doreau *et al.* (1985), Kay (1987), Holtenius and Björnhag (1989), Hofmann and Nygren (1992), Woodall and Skinner (1993), Wang *et al.* (1998),Clauss *et al.* (2003, 2006a, 2006b), Hofmann *et al.* (2008), Pérez *et al.* (2009), Clauss *et al.* (2010), Górka *et al.* (2011), Lin *et al.* (2011), Pérez and Jerbi (2012), Pérez and Vazquez (2012), Meyer *et al.* (2014), Mitchell et al. (2015) and Krämer (unpublished). In a few species, data from more than one source was available. In such cases, a weighted average of

BM and the anatomical measure was calculated based on the number of animals included in each study.

To determine the relation between BM and anatomical measures in the giraffe, data were ln-transformed and allometric regression analysis was used to determine the coefficients of the model: $\ln(\mathrm{Y}) = \alpha + \beta \text{ x } \ln(BM)$, where Y = the anatomical measure and BM = body mass in kg. Origin of the giraffes (wild or captive) was not included as an explanatory variable in the model due to a limited overlap in BM range. There did not appear to be any systematic differences in any of the anatomical measures between zoo and wild giraffes, when inspecting the data graphically. The one exception to this was reticulum height and width measures, which were substantially less and with greater variation in the zoo giraffes. Thus, for the two reticulum measures, data from captive giraffes (n = 4) were excluded from the data set. Data from the two calves were not included in the regression analysis of any of the measures. The hypothesis of isometric scaling was accepted if 0.33, 0.67 and 1.00 was included in the 95% confidence interval (CI) of the BM exponent (β) of dimensions, areas and weights, respectively.

To compare giraffes to domestic cattle as well as 'moose-type' ruminants to 'cattle-type' ruminants in general, species (giraffe or cattle) or digestive tract type ('moose-' or 'cattle-type') was added as an explanatory variable to the allometric regression model described above, i.e., $\ln(\mathrm{Y}) = \alpha + \beta \text{ x } \ln(BM) + \gamma \text{ x } (species\ or\ digestive\ tract\ type)$.

ANOVA was used for step-wise model reduction. All statistical analyses were performed using the statistical software R, version 2.15.0 (R Development Core Team, Vienna, Austria, 2012). The significance level was set to 0.05, with values up to 0.10 considered as trends.

Results and discussion

The stomach of the giraffe was comprised of a rumen, reticulum, omasum and abomasum as in all other true ruminants (Figure 1 and 2a-d). The rumen was the largest compartment followed by the abomasum, then the reticulum and the omasum, which is in agreement with previous findings in giraffes (Hofmann, 1973). The stomachs of the two calves followed the same pattern, though the size of the abomasum in relation to the forestomachs was much greater (Figure 2d). Reticuloruminal tissue weight and all external rumen dimensions were positively related to BM, whereas external reticulum dimensions were not affected by BM ($p > 0.1$; Table 2). Internally, reticular crest height was positively related to BM, while the caudal ruminal pillar thickness only tended to correlate positively to BM ($p = 0.056$, Table 2). Thickness of the cranial ruminal pillar was independent of

BM ($p = 0.233$). The absence of a significant effect of BM on ruminal pillar thickness indicates that these structures are rather fixed, while the rumen wall is continuously expanding. Omasal leaves of first, second, and third order were identified in all giraffes investigated, while only very few fourth order leaves were sporadically observed. The first, second and third order leaves were present in the repeated sequence of 1st -3rd -2nd -3rd, see Figure 2E. All omasal and abomasal measures scaled positively to BM (Table 3 and 4). Tissue weights and lengths of the SI, cecum and total LI (cecum, colon and rectum) all correlated positively to BM, while the ratio of SI : total LI length decreased with increasing BM (Table 5), which means that the total LI was relatively longer in larger animals. The weight of both the parotid and mandibular salivary glands scaled positively to BM (Table 6). The shape and position of the glands are shown on Figure 3; for another drawing of giraffe salivary glands, see Pérez et al. (2012). The BM scaling exponents (with 95% CI in brackets) of salivary gland weight were 1.33 [1.04 – 1.63] for the parotid glands and 0.70 [0.11 – 1.28] for the mandibular glands. Based on geometric considerations, it was hypothesized that these weights would scale to $BM^{1.00}$ within the species. Note that across species, Hofmann *et al.* (2008) found salivary gland weight to be related to metabolic body mass, i.e., $BM^{0.75}$.

Some of the anatomical measurements documented in this study have previously been described in giraffes. Previous intestinal length measurements were generally comparable with data from this study (Table 7). Salivary gland weights were similar to those reported for 9 wild giraffes in a recent study (Mitchell *et al*., 2015), as well as for one captive adult giraffe of unknown body mass (Pérez *et al*., 2012), while another study observed heavier glands in 3 captive giraffes (Hofmann *et al*., 2008) (Fig. 6). The wild giraffes in this study were captured in private game reserves, and kept in captivity for approximately 2 months prior to weighing and dissecting. Although the diet was similar to that of wild giraffes, these animals probably ate less than what they would have in the wild, because of stress and/or reduced palatability of the diet, with subsequent weight loss as a result. Visually, the majority of the wild giraffes were in poor body condition and nearly all had depleted fat stores, with little to no intestinal fat, as has been reported in poorly adapted captive animals (Potter and Clauss, 2005). The zoo giraffes were all in a good to moderately overweight condition. The condition of the giraffes presumably influenced the size of their digestive tracts, as these organs are metabolically expensive and therefore likely reduced in size to some extent during prolonged periods of low nutrient availability, which has been demonstrated in fasting studies with domestic ruminants (e.g., in cattle (Carnegie *et al.*, 1969) and sheep (Aziz *et al.*, 1993)). Thus, both the BM and GI tract mass may have been reduced in the wild caught giraffes, but not necessarily to the same extent. In addition, gastrointestinal organ weights are highly susceptible to differences in dissection methods, which might also contribute to variation between studies. Dissection protocols should be clearly stated, for instance with regard to level of trimming away of associated tissues, rinsing with water and drying procedures. In this study, great care was taken to trim and clean the organs before weighing, which may contribute to the lower reticulorumen tissue and salivary gland weight found in this study.

The scaling exponent of BM was as expected for all measures, except for total LI length, and weight of the parotid glands and SI tissue. Since SI length scaled to BM as expected, but the SI tissue weight scaling was lower, the thickness of the tissue must decrease as the intestines elongates in ontogeny. A decrease in tissue mass with elongation was observed for LI as well, where the BM scaling exponent was higher for length than for tissue weight. Although the expected isometric scaling exponent was within the 95% CI of the BM exponent of most measures, some had a very wide CI range. For reticular crest height, the wide variation in 95% CI was caused by a large captive male included in the study as it had much higher crests (6 mm) than any other giraffe in the study (1.0 – 2.5 mm). If this outlier was excluded from the data set, reticular crest height was no longer correlated to BM (see footnote in Table 2). Excluding this male, captive giraffes (n = 2, range: 1.2 – 2.0 mm) did not seem to have higher reticular crests than wild giraffes (n = 15, range: 1.0 – 2.5 mm). Though not statistically testable, this is contrary to the findings of Hofmann and Matern (1988) who found that two captive giraffes had higher and more subdivided crests compared to wild giraffes, and described this finding as resembling that of grass-eating intermediate feeding ruminants. For wild giraffes, Hofmann (1973) noted reticular crest heights of 1 – 3 mm, as observed in this study. The scarcity of data does not allow conclusions about an influence of captivity on this measure; it is simply noted that outlying values have been reported for reticular crest height in captive giraffes.

Although this study includes data from a total of 38 giraffes, data from very young animals (<1 year of age), as well as from very large animals (>900 kg), were few in the data set. This should be kept in mind when predicting the size of a given anatomical measure from the BM of a giraffe, especially if the regression line is extrapolated to animals beyond the BM range covered in the data set. For wild giraffes, the range of body masses covered was only 280 to 660 kg. As an indirect result of this, data from giraffes of different origin, as well as of different subspecies, were pooled. Since diet has been documented to alter some measures of digestive anatomy in giraffes (Hofmann and Matern, 1988) and other ruminants (e.g., cattle (Lauwers, 1973), sheep (McLeod and Baldwin, 2000) and reindeer (Mathiesen *et al.*, 2000)), there might be diet-related differences in the digestive anatomy between wild and captive giraffes. Although Hofmann (1973) found "*no significant anatomical differences, in* *the digestive tract, between the two subspecies*" of sampled wild giraffes, the different subspecies of giraffes may differ to some extent in their digestive anatomy as well. Thus, to be able to compare the digestive anatomy of captive and free-ranging giraffes, ideally these should be of the same subspecies as well as cover the entire BM range from newborn to 1500 kg.

Based on knowledge of the natural diet of giraffes (Leuthold and Leuthold, 1972; Sauer *et al.*, 1977; Pellew, 1984), as well as previous qualitative and quantitative descriptions of their digestive anatomy (e.g., Hofmann, 1988), giraffes were hypothesized to have a 'moose-type' digestive tract, as characterized by smaller rumens and lower reticular crests (Clauss *et al.*, 2010b), thinner ruminal pillars (Clauss *et al.*, 2003), smaller omasal laminar surface area (Clauss *et al.*, 2006b) and larger parotid salivary glands (Robbins *et al.*, 1995; Hofmann *et al.*, 2008) than 'cattle-type' ruminants of similar size. When plotted against existing data on digestive anatomy of other ruminant species, giraffes clearly belonged with the other 'moose-type' ruminants with regard to ruminal pillar thickness, reticular crest height and omasal laminar surface area (Figure 4). All three measures were lower in 'moose-type' than 'cattle-type', with p-values <0.01. Giraffe data supported the positive correlation between BM and rumen height, while difference in rumen height between digestive tract types only tended towards significance (p = 0.061, Figure 4). Giraffe data supported the positive correlation of BM to intestinal lengths in all three measures. Neither SI, cecum and nor the ratio of SI : total LI length differed significantly between 'moose-type' and 'cattle-type' ruminants (p-values of 0.530, 0.434, and 0.392 respectively), while there was only a tendency for total LI length to be longer in 'moose-types' (p = 0.070) (Figure 5). In addition to the 'moose-type' forestomach measures observed in this study, data from Mitchell et al. (2015) place the giraffe in the low end of the relative masseter muscle weight range reported for ruminants (Clauss *et al.*, 2008), which corroborate the finding by the earlier study that browsing ruminants have lower masseter muscle weight than grazing ruminants.

Both the parotid and mandibular salivary glands were larger in 'moose-type' compared to 'cattle-type' ruminants (p <0.001), but the giraffe salivary glands were in the weight range of 'cattle-types' rather than of 'moose-types' (Figure 6). Clauss *et al.* (2006a) found captive okapi to have smaller salivary glands than expected as well, reported an unpublished observation of comparatively small salivary glands in two captive giraffes, and hypothesized that relatively small salivary glands might be a family trait of the giraffids. This hypothesis is further supported by the present study. In addition, Robbins *et al.* (1995) found that another strict browse-eating ruminant, the greater kudu had 'grazer-size' parotid salivary glands, while other browsing members of the Tragelaphus family (the nyala and the bushbuck) had parotid glands of a size expected for ruminants of intermediate feeding type. Hofmann *et al.* (2008) described somewhat larger salivary glands in greater kudu, but stressed that within the group of the Bovinae (Bovini and Tragelaphini), deviations from the typical relationship with the natural diet are apparent. Similarly, Clauss and Hofmann (2014) outlined that members of the Bovini have by far the largest omasa among ruminants but are not the most extreme grazers. Hence, deviation from the overall relationship between natural diet and morphological variables, such as salivary gland size (Jiang and Takatsuki, 1999; Hofmann *et al.*, 2008), may occur due to phylogenetic affiliation and possibly contribute to the scatter evident in such relationships. Therefore, morphological measures might indicate convergence with respect to the natural diet, but might often not be suitable as predictors of that diet for a specific species. Looking at the original data set behind the salivary gland weight dichotomy hypothesis (Hofmann *et al.*, 2008), data for all species of grazers originate from either one (14 species) or two (8 species) individual animals of each species, while the same is true for 50% of the browsing species. This makes the data set very vulnerable to naturally occurring biological variation, as was seen in this study (parotid glands weighed 222 ± 125 g, Table 6). Thus, data from a larger number of individuals of the various species should be added to the data set to confirm the hypothesis of salivary gland dichotomy between feeding types.

When compared solely to domestic cattle over a range of body masses, i.e., ranging from calves to adult animals, giraffes had lower tissue weight of all stomach compartments (all p-values <0.001, Figure 7), indicating a smaller relative capacity of the stomachs in the giraffe. In addition, giraffes had longer total LI length and lower SI : total LI length ratio (both p-values <0.001, Figure 7), while there was no difference in SI and cecum length (both p-values >0.130). The absence of a difference in cecum length is in contrast to the hypothesis that feeding types differ in this measure (Hofmann, 1989). The observation of a longer LI is in accordance with the evident difference in moisture content between fecal pellets of giraffes and ‘pie-like’ feces of cattle and other Bovini (Clauss *et al.*, 2004), implicating a less efficient re-absorption of water from the LI of the Bovini. In general, measures of the intestines do not support systematic differences between ruminant feeding types (Figure 5 and Pérez *et al.*, 2008), suggesting little potential of these measures to serve as predictors of natural diet and little relevance with respect to adaptations to different diets (as opposed to adaptations to different habitats).

In conclusion, the majority of anatomical measures scaled to BM as expected in giraffes. When compared specifically to domestic cattle, the tissue weight of the stomachs was lower in giraffes, while the total LI were longer. The digestive system of the giraffe displayed many of the 'moose-type' morphological characteristics such as thin ruminal pillars, low reticular crests and relatively small surface area of the omasal leaves, however, salivary gland weight was in the range of 'cattle-types' rather than of other 'moose-types'. These findings underline the potential relevance of phylogeny on morphological measures that may or may not overrule signals considered indicative of convergence, and emphasize the need for large comparative datasets for the demonstration of such convergences.

Abbreviations

BM = body mass, CI = confidence interval, GI = gastrointestinal, LI = Large intestine, SI = small intestine, total LI = cecum, colon and rectum.

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Conflict of interest

The authors have no conflict of interest regarding the content of this manuscript.

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Tables

Table 1: Information about giraffes included in the study

Sub-species	Year	Males	Origin	Females	Origin
Southern giraffe, *G. c. giraffa*	2006	280 kg (1 y), 360 kg (1.5 y), 370 kg (2 y), 450 kg (2.5 y), 470 kg (2.5 y) and 490 kg (3 y)	a	-	-
	2010	330 kg (1 y), 380 kg (1.5 y), 398 kg (2.5 y) 425 kg (2 y), 450 kg (2.5 y), 451 kg (2 y), 456 kg (3 y), 460 kg (2.5 y), 475 kg (3.5 y), 490 kg (3.5 y), 503 kg (2 y), 527 kg (2.5 y), 603 kg (4 y), 630 kg (4.5) and 654 kg (4 y)	a	490 kg (3.5 y)	a
	2012	415 kg (3 y), 462 kg (3 y), 550 kg (4 y) and 660 kg (4 y)	a	-	-
Reticulated giraffe, *G. c. reticulata*	2013	470 kg (2 y)	b	-	-
	2014	61 kg (4 d), 550 kg (2 y)	c	182 kg (8 m) and 700 kg (24 y)	d
Rothschild's giraffe, *G. c. rotchildi*	2013	664 kg (3 y), 1225 kg (18 y)	e	-	-
	2014	62 kg (9 d)	e	-	-
Hybrid	2012	535 kg (3 y)	f	690 kg (17 y), 792 kg (5 y) and 825 kg (5 y)	g, h, h
	2013	574 kg (1.5 y)	f		

Abbreviations used: *G. c* = *Giraffa camelopardalis*, y = year, m = months, d = days.
a = wild caught in Namibia or South Africa; b = Odense Zoo, Denmark; c = Copenhagen Zoo, Denmark; d = Kolmården Djurpark, Sweden; e = Givskud Zoo, Denmark; f = Ree Safari Park, Denmark; g = Jyllands Park Zoo, Denmark; and h = Knuthenborg Safari Park, Denmark.

Table 2. Equations for determination of rumen and reticulum size measures related to body mass of giraffes

Measure	Unit	n	BM [range] (kg)	Mean ± SD	Effect of BM	Model[1], Y= α * BM$^{\beta}$	R^2
Reticulorumen tissue weight	kg	24	552.2 [182 – 1225]	6.1 ± 2.6	P < 0.001	0.01 [0.00 ; 0.05] * BM$^{1.00\ [0.76\ ;\ 1.24]}$	0.78
Rumen height	cm	19	532.2 [182 – 1225]	87.7 ± 13.8	P < 0.001	8.72 [4.17 ; 18.14] * BM$^{0.37\ [0.25\ ;\ 0.49]}$	0.72
Dorsal rumen length	cm	19	532.2 [182 – 1225]	68.3 ± 13.7	P < 0.001	7.40 [2.33 ; 23.49] * BM$^{0.36\ [0.17\ ;\ 0.54]}$	0.49
Ventral rumen length	cm	19	532.2 [182 – 1225]	62.5 ± 9.5	P < 0.001	9.06 [3.43 ; 23.89] * BM$^{0.31\ [0.15\ ;\ 0.47]}$	0.51
Total rumen diagonal	cm	19	532.2 [182 – 1225]	74.7 ± 12.5	P < 0.001	7.70 [3.22 ; 18.42] * BM$^{0.36\ [0.22\ ;\ 0.50]}$	0.64
Reticulum height[2]	cm	14	473.5 [330 – 654]	30.9 ± 4.3	P = 0.136	4.46 [0.32 ; 61.58] * BM$^{0.31\ [-0.11\ ;\ 0.74]}$	0.18
Reticulum length[2]	cm	14	473.5 [330 – 654]	29.6 ± 4.2	P = 0.241	5.41 [0.27 ; 107.26] * BM$^{0.28\ [-0.21\ ;\ 0.76]}$	0.11
Reticular crest height[3]	mm	21	519.5 [330 – 1225]	1.6 ± 1.1	P = 0.032	0.01 [0.00 ; 0.88] * BM$^{0.79\ [0.08\ ;\ 1.50]}$	0.22
Cranial rumen pillar thickness	mm	15	515.9 [182 – 1225]	6.5 ± 2.4	P = 0.233	1.06 [0.05 ; 22.0] * BM$^{0.28\ [-0.21\ ;\ 0.78]}$	0.11
Caudal rumen pillar thickness	mm	15	515.9 [182 – 1225]	8.3 ± 2.1	P = 0.056	0.81 [0.08 ; 8.61] * BM$^{0.37\ [-0.01\ ;\ 0.75]}$	0.25

Abbreviations used: BM = body mass, SD = standard deviation.
[1]95% confidence interval for each estimate in brackets [min ; max].
[2]Only wild giraffes included in data set.
[3]When excluding a single large male from the data set, mean reticular crest height was 1.4 ± 0.5, model parameters changed to 3.46 [0.02 ; 759.63] * BM$^{-0.16\ [-1.03\ ;\ 0.72]}$ (R^2 = 0.01). The effect of BM was no longer significant (P = 0.711).

Table 3: Equations for determination of omasum size measures related to body mass of giraffes

Measure	Unit	n	BM [range] (kg)	Mean ± SD	Effect of BM	Model[1], Y= α * BM$^{\beta}$	R^2
Omasum tissue weight	g	30	524.4 [182 – 1225]	806 ± 381	P < 0.001	0.61 [0.12 ; 3.04] * BM$^{1.14\ [0.88\ ;\ 1.40]}$	0.74
Omasum height	cm	26	549.6 [182 – 1225]	20.0 ± 4.5	P < 0.001	1.65 [0.49 ; 5.51] * BM$^{0.40\ [0.20\ ;\ 0.59]}$	0.43
Omasum length	cm	26	549.6 [182 – 1225]	15.6 ± 4.1	P = 0.007	1.39 [0.26 ; 7.47] * BM$^{0.38\ [0.11\ ;\ 0.65]}$	0.26
Omasum curvature	cm	32	524.0 [182 – 1225]	40.3 ± 9.0	P = 0.002	4.73 [1.37 ; 16.38] * BM$^{0.34\ [0.14\ ;\ 0.54]}$	0.29
Number of laminae omasi	-	30	524.4 [182 – 1225]	57 ± 6	P = 0.002	19.12 [10.07 ; 36.28] * BM$^{0.18\ [0.07\ ;\ 0.28]}$	0.30
Total omasal laminar surface area	cm^2	28	523.7 [182 – 1225]	5075 ± 1716	P < 0.001	40.15 [8.89 ; 181.34] * BM$^{0.77\ [0.53\ ;\ 1.01]}$	0.62

Abbreviations used: BM = body mass, SD = standard deviation.
[1]95% confidence interval for each estimate in brackets [min ; max].

Table 4. Equations for determination of abomasum size measures related to body mass of giraffes

Measure	Unit	n	BM [range] (kg)	Mean ± SD	Effect of BM	Model[1], Y= α * BM$^{\beta}$	R^2
Abomasum tissue weight	g	26	550.2 [182 – 1225]	1275 ± 635	P < 0.001	1.26 [0.20 ; 7.83] * BM$^{1.09\ [0.80\ ;\ 1.38]}$	0.71
Greater abomasum curvature length	cm	18	538.9 [182 – 1225]	71.6 ± 12.3	P = 0.041	18.0 [4.89 ; 66.41] * BM$^{0.22\ [0.01\ ;\ 0.43]}$	0.24
Lesser abomasum curvature length	cm	19	547.4 [182 – 1225]	41.2 ± 8.2	P = 0.002	3.96 [1.02 ; 15.36] * BM$^{0.37\ [0.16\ ;\ 0.59]}$	0.43

Abbreviations used: BM = body mass, SD = standard deviation.
[1]95% confidence interval for each estimate in brackets [min ; max].

Table 5. Equations for determination of intestinal size measures related to body mass of giraffes

Measure	Unit	n	BM [range] (kg)	Mean ± SD	Effect of BM	Model[1], Y= α * BM^{β}	R^2
Small intestine tissue weight	g	25	552.1 [182 – 1225]	2678 ± 800	P < 0.001	52.2 [16.69 ; 163.44] * BM$^{0.62\ [0.44\ ;0.81]}$	0.69
Small intestinal length	m	22	559.2 [182 – 1225]	39.1 ± 6.1	P = 0.004	8.40 [3.14 ; 22.47] * BM$^{0.24\ [0.09\ ;\ 0.40]}$	0.34
Total large intestine[2] tissue weight	g	24	552.8 [182 – 1225]	4001 ± 1714	P < 0.001	4.61 [1.22 ; 17.31] * BM$^{1.07\ [0.86\ ;\ 1.28]}$	0.83
Total large intestine[2] length	m	21	553.0 [182 – 1225]	16.6 ± 4.4	P < 0.001	0.38 [0.14 ; 1.05] * BM$^{0.60\ [0.44\ ;\ 0.76]}$	0.76
Cecum tissue weight	g	14	501.5 [330 – 690]	256 ± 929	P = 0.012	0.15 [0.00 ; 0.04] * BM$^{1.19\ [0.31\ ;\ 2.08]}$	0.42
Cecum length	cm	19	532.2 [182 – 1225]	50.4 ± 15.7	P = 0.048	4.28 [0.39 ; 47.16] * BM$^{0.39\ [0.00\ ;\ 0.78]}$	0.21
SI : total LI length ratio	-	21	553.0 [182 – 1225]	2.4 ± 0.5	P = 0.002	21.80 [5.99 ; 79.31] * BM$^{-0.35\ [-0.56\ ;\ -0.15]}$	0.40

Abbreviations used: BM = body mass, SD = standard deviation, SI = small intestines, LI = large intestines.
[1]95% confidence interval for each estimate in brackets [min ; max].
[2]Total large intestine was defined as cecum, colon and rectum.

Table 6. Equations for determination of salivary gland weight related to body mass of giraffes

Measure	Unit	n	BM [range] (kg)	Mean ± SD	Effect of BM	Model[1], Y= α * BM^{β}	R^2
Glandula parotis weight (pair)	g	13	569.7 [380 – 1225]	202 ± 131	P < 0.001	0.04 [0.01 ; 0.26] * BM$^{1.33\ [1.04\ ;\ 1.63]}$	0.90
Glandula mandibularis weight (pair)	g	12	581.8 [380 – 1225]	143 ± 50	P = 0.024	1.64 [0.04 ; 66.65] * BM$^{0.70\ [0.11\ ;\ 1.28]}$	0.41

Abbreviations used: BM = body mass, SD = standard deviation.
[1]95% confidence interval for each estimate in brackets [min ; max].

Table 7: Existing data on anatomical measures of the digestive system of giraffes compared to findings of this study

	Unit	This study	Pérez *et al.* (2009)	Beddard (1902), Richiardi (1880), and Owen (1839)	Crisp (1864a, 1864b)
Animals		n = 12 – 23	n = 2	n = 5 (est.[1])	n = 4
Age		1.5 – 24.5 y	1 juv. / 1 adult	3 – 4 y + unkn.[1]	2 juv. + 2 adults
Body mass	kg	380 – 1225	754 / 800	-	150 – 800
Small intestinal length	m	30.6 – 55.5	28 / 47	25 – 60	-
Cecum length	cm	27 – 89	44 / 96	65 – 76	-
Large intestinal length	m	10.5 – 28.6	23.8 / 24.3	12 – 24	-
SI: total LI[2] length ratio	-	1.5 – 3.5	1.1 / 2.0	2.1 – 2.6	-
Total intestinal length	m	41.4 – 75.4	52 / 71	-	38 – 70

Abbreviations used: est. = estimate, y = year, juv. = juvenile, unkn. = unknown, SI: = small intestine, LI = large intestine.
[1]Owen report n = 3 of age three – four years, but the other two authors do not report number or age of animals.
[2] Total large intestine = cecum, colon and rectum.

Figure captions

Figure 1: The gastrointestinal tract of a captive 195 kg juvenile male giraffe. The dotted lines mark the points of separating the different digestive tract sections, RR = reticulorumen, O = omasum, AB = abomasum, SI = small intestine, CE = cecum and LI = large intestines (colon + rectum).

Figure 2: Giraffe stomachs with measuring points for the anatomical measures depicted.
2a) 490 kg female, ~3.5 years, wild caught. 1 = rumen height, 2 = dorsal rumen length, 3 = ventral rumen length. 2b) 700 kg female, ~24 years, captive. 4 = rumen diagonal, 5 = reticulum length, 6 = reticulum height, 7 = omasum curvature. 2c) 800 kg female, ~17.5 years, captive. 8 = omasum length, 9 = omasum height. 2d) 62 kg male, 9 days, captive. 10 = abomasum greater curvature, 11 = abomasum lesser curvature. 2e) 195 kg male, ~1.5 years, captive. Cross section of a giraffe omasum. Omasal laminae of first, second and third order are marked with I, II and III, respectively.

Figure 3: Position of the parotid and mandibular salivary glands of the giraffe. The mandibular glands were positioned medially to the parotid glands. Courtesy of Jeanne Peter.

Figure 4: Allometric regression of correlation between selected forestomach measures, body mass and ruminant feeding type. Giraffe data from this study (grey circles) and Clauss *et al.* (2003, 2006b, 2010) (grey circle with x). Data from other ruminant species from Hofmann and Nygren (1992), Clauss *et al.* (2003, 2006a, 2006b, 2010), Pérez and Jerbi (2012), and Pérez and Vazquez (2012). Each species is represented by a point, except for the giraffe. Solid line: trendline for ‘moose-type’ ruminants (not including giraffe), dashed line: trendline for ‘cattle-type’ ruminants.

Figure 5: Allometric regression of correlation between intestinal length, body mass and ruminant feeding type. Giraffe data from this study (grey circles) and Pérez *et al.* (2009) (grey circle with x). Data from other ruminant species from Hofmann and Nygren (1992), Woodall and Skinner (1993), Clauss *et al.* (2006a), Lin *et al.* (2011), Pérez and Vazquez (2012), and Krämer (unpublished; data on cattle). Each species is represented by a point, except for the giraffe. Solid line: trendline for ‘moose-type’ ruminants (not including giraffe), dashed line: trendline for ‘cattle-type’ ruminants.

Figure 6: Allometric regression of correlation between salivary gland weight, body mass and ruminant feeding type. Giraffe data from this study (grey circles), Hofmann *et al.* (2008) (grey circle with x) and Mitchell et al. (2015) (grey circle with +). Data from other ruminant species from Kay (1987), Clauss *et al.* (2006), and Hofmann *et al.* (2008). Each species is represented by a point, except for the giraffe. Solid line: trendline for 'moose-type' ruminants (not including giraffe), dashed line: trendline for 'cattle-type' ruminants.

Figure 7: Allometric regression of correlation between body mass and selected anatomical measures in giraffes and cattle. Giraffe data from this study (black circles). Cattle data from Tamate *et al.* (1962), Tulloh (1966), Doreau *et al.* (1985), Holtenius and Björnhag (1989), Wang *et al.* (1998), Górka *et al.* (2011), Meyer *et al.* (2014), and Krämer (unpublished). Each measure represents either individual animals (all giraffe data and total LI length for cattle) or mean body mass and tissue weight reported in individual studies. Solid line: trendline for giraffes, dashed line: trendline for cattle.

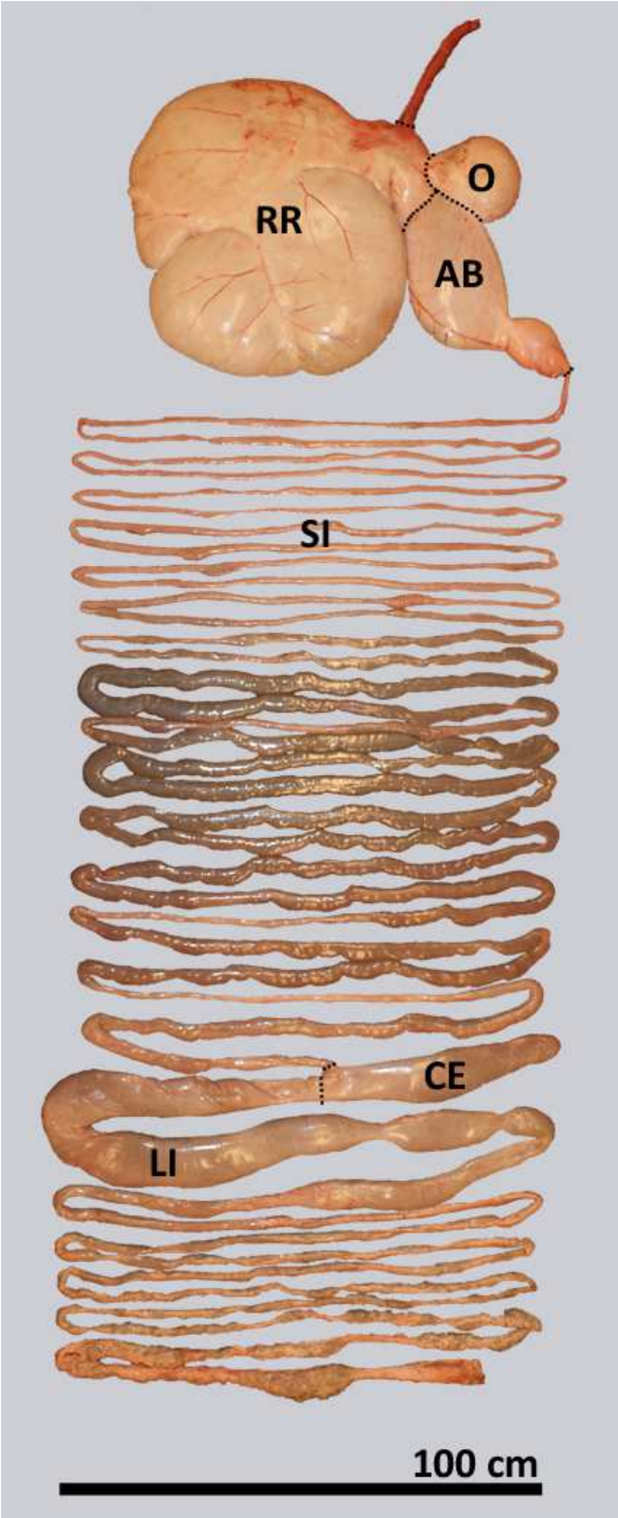


Figure 1

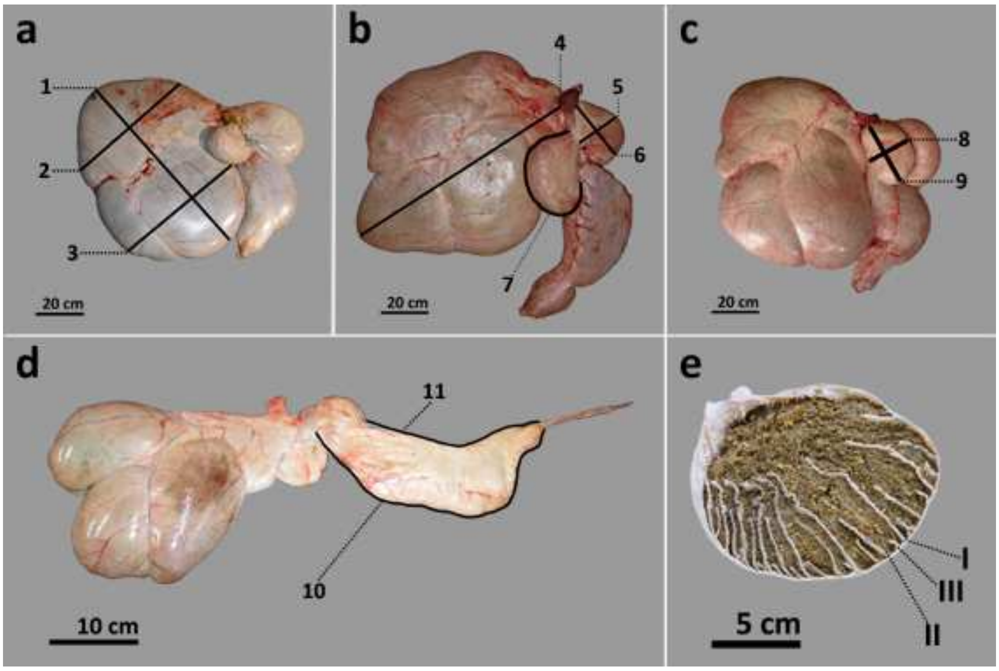


Figure 2

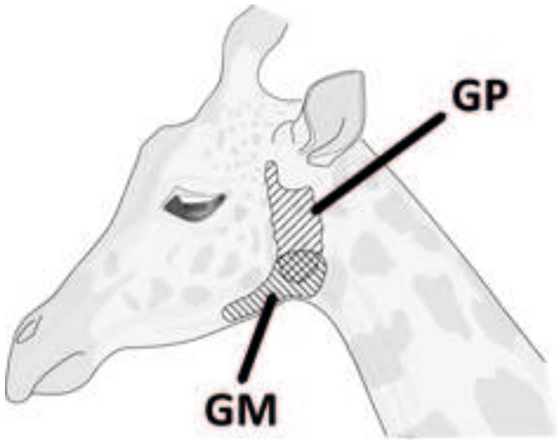


Figure 3

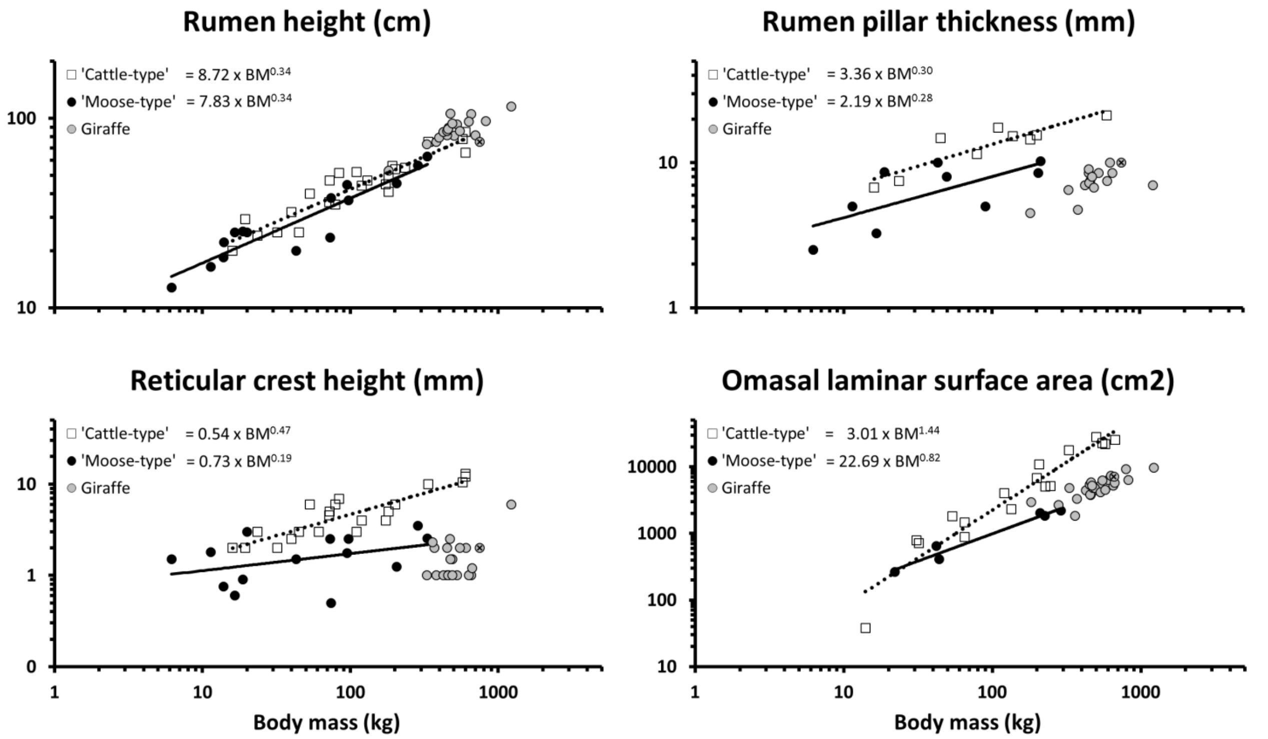
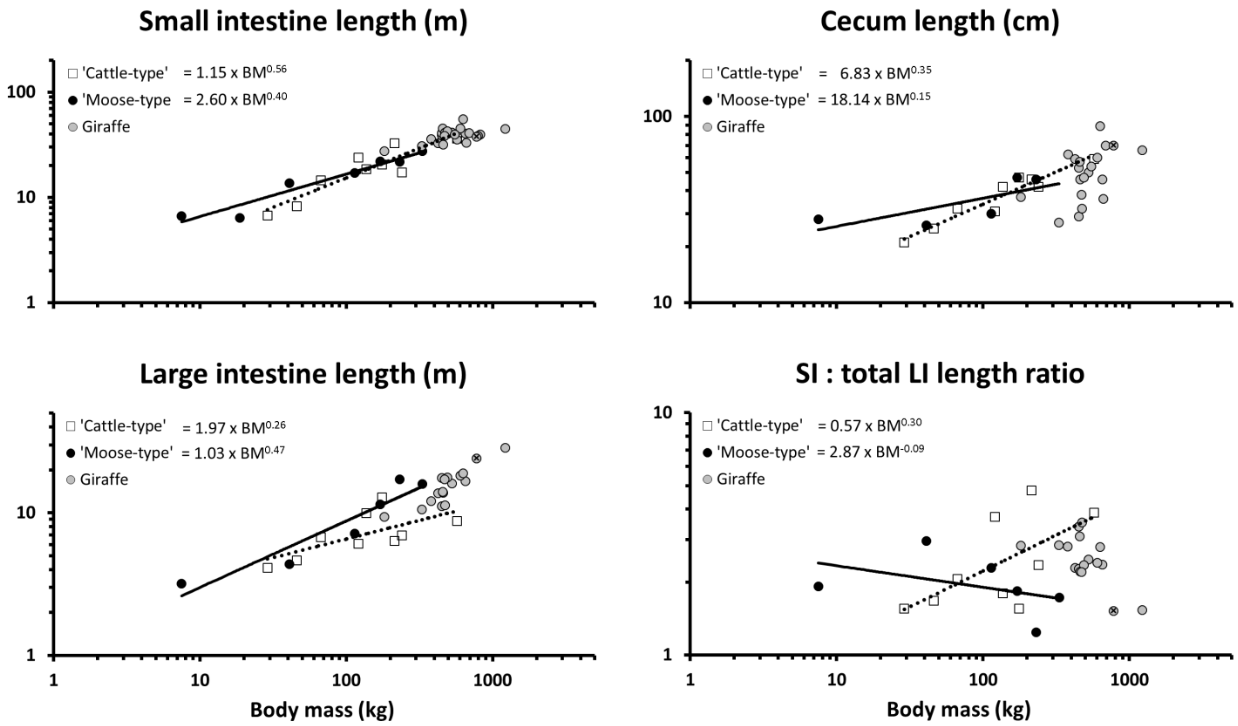
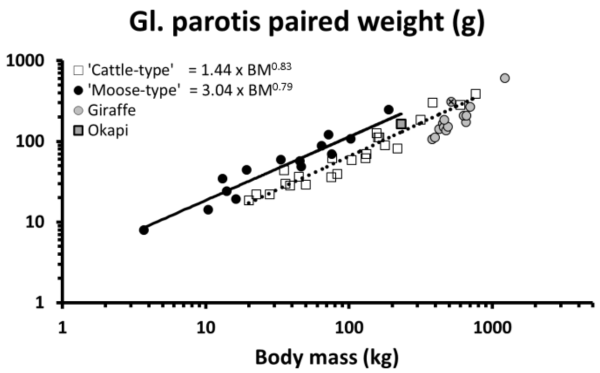

Rumen height (cm)
□ 'Cattle-type' = 8.72 x BM0.34
● 'Moose-type' = 7.83 x BM0.34
● Giraffe
Rumen pillar thickness (mm)
□ 'Cattle-type' = 3.36 x BM0.30
● 'Moose-type' = 2.19 x BM0.28
● Giraffe
Reticular crest height (mm)
□ 'Cattle-type' = 0.54 x BM0.47
● 'Moose-type' = 0.73 x BM0.19
● Giraffe
Omasal laminar surface area (cm2)
□ 'Cattle-type' = 3.01 x BM1.44
● 'Moose-type' = 22.69 x BM0.82
● Giraffe
Body mass (kg)
Body mass (kg)

Figure 4



Small intestine length (m)
'Cattle-type' = 1.15 x BM0.56
'Moose-type' = 2.60 x BM0.40
Giraffe
Cecum length (cm)
'Cattle-type' = 6.83 x BM0.35
'Moose-type' = 18.14 x BM0.15
Giraffe
Large intestine length (m)
'Cattle-type' = 1.97 x BM0.26
'Moose-type' = 1.03 x BM0.47
Giraffe
SI : total LI length ratio
'Cattle-type' = 0.57 x BM0.30
'Moose-type' = 2.87 x BM-0.09
Giraffe
Body mass (kg)
Body mass (kg)

Figure 5


Gl. parotis paired weight (g)
'Cattle-type' = 1.44 x BM0.83
'Moose-type' = 3.04 x BM0.79
Giraffe
Okapi
1000
100
10
1
1
10
100
1000
Body mass (kg)

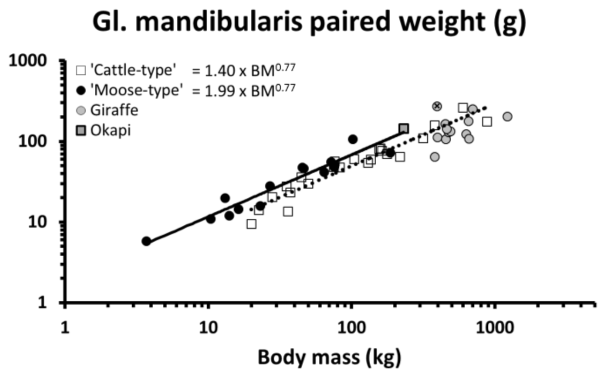

Gl. mandibularis paired weight (g)
'Cattle-type' = 1.40 x BM0.77
'Moose-type' = 1.99 x BM0.77
Giraffe
Okapi
1000
100
10
1
1
10
100
1000
Body mass (kg)

Figure 6

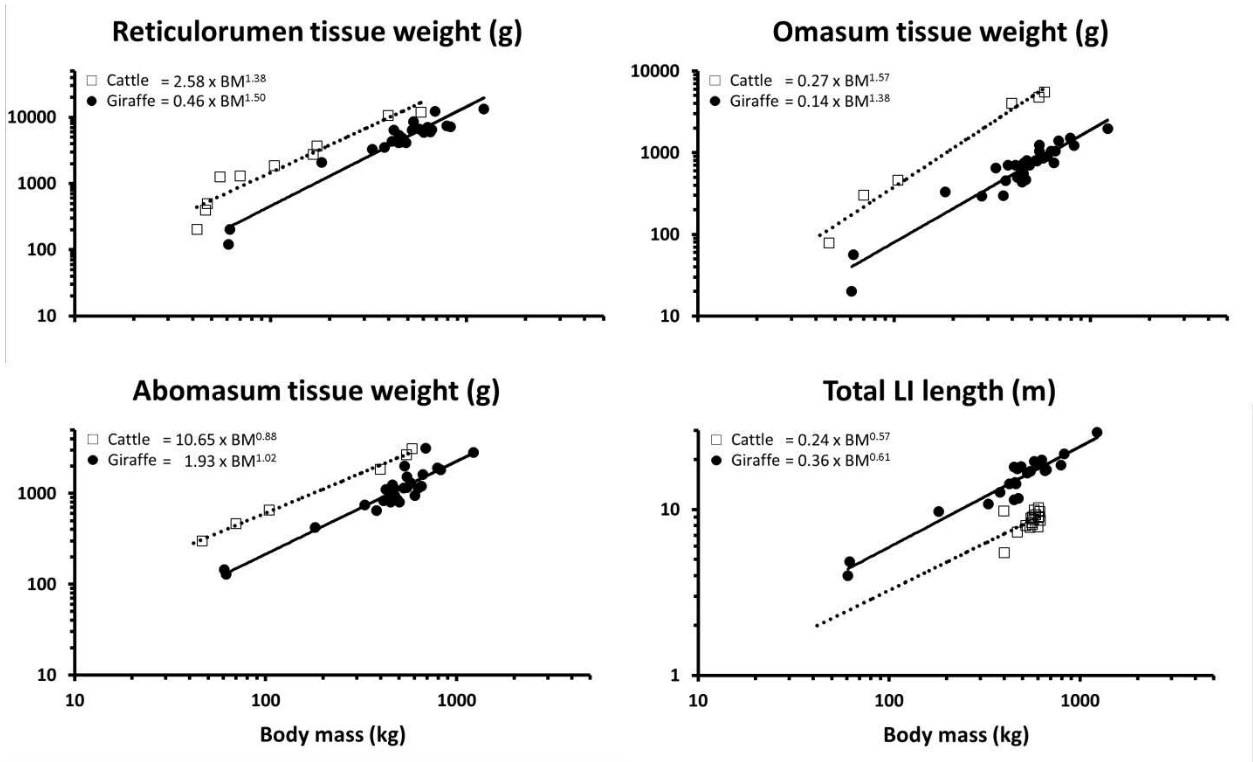

Reticulorumen tissue weight (g)
Cattle = 2.58 x BM1.38
Giraffe = 0.46 x BM1.50
Omasum tissue weight (g)
Cattle = 0.27 x BM1.57
Giraffe = 0.14 x BM1.38
Abomasum tissue weight (g)
Cattle = 10.65 x BM0.88
Giraffe = 1.93 x BM1.02
Total LI length (m)
Cattle = 0.24 x BM0.57
Giraffe = 0.36 x BM0.61
Body mass (kg)
Body mass (kg)

Figure 7